# PROBLEMS IN USING THE LINCOLN INDEX FOR ESTIMATING THE SIZE OF ANT COLONIES (HYMENOPTERA: FORMICIDAE)

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Received for Publication April 18, 1962

**ABSTRACT**

A number of foraging ants in colonies of known sizes were marked and samples of the foraging population were taken at intervals thereafter. The theoretical population of the colony was calculated from the number of marked and unmarked workers obtained in these samples. Under the conditions of these experiments it was shown that about 80 per cent of the ants did not participate in foraging and hence samples of the foraging population cannot be used to obtain estimates of the whole population. Factors affecting foraging by ants are discussed in relation to this mark-release-recapture method of estimating populations.

## Introduction

The Lincoln Index, a method of estimating animal populations, was recommended by Chew (1959) for estimating the size of ant colonies. As used by him the method was to collect and mark a known number of ants from one colony. The ants were returned to the nest entrance and a second sample of workers was taken 24 hours later. For an estimate of the colony size the number of marked and unmarked workers in the second sample were used in the formula

$$\frac{(\text{No. ants in 2nd sample}) \times (\text{Total no. marked})}{\text{Number of marked ants recaptured}}.$$

The accuracy of this formula depends on the assumptions that all ants in the colony are equally susceptible to capture, that the marked ants mix thoroughly with the unmarked, and that the marking is permanent and has no adverse influence on the ants during the length of the sample period.

Chew admitted that, because of the existence of specialized castes, e.g., the repletes of *Myrmecocystus* species, the first assumption is not always permissible, and hence the method is not suitable for certain species. However, he claimed that the exceptions are few and do not limit the application of the method to most North American species of ants. I feel, however, that until much more is known of the foraging behaviour of ants this assumption is not valid for any species, and that the Lincoln Index is of doubtful value in estimating colony size.

The following is an analysis of the use of this method based on laboratory experiments with three species of Formicinae and on the known behaviour patterns of other species of ants.

## METHODS

Colonies of *Formica fusca* (Linné), *F. exsectoides* Forel, and *Camponotus herculeanus* (Linné) of known sizes were reared in a laboratory at 23° C. and 50 per cent R.H. Though the structure and design of the nests varied slightly each had an inner partitioned chamber cooled to 12° C. and an outer unpartitioned chamber at room temperature (23° C.). The foraging area of each colony of *F. fusca* and *C. herculeanus* was 2 by 4 feet; that of *F. exsectoides* was 8 by 12 inches. All colonies were fed unlimited amounts of 50 per cent honey solution and house fly larvae.

Approximately 25 per cent of all foraging workers were marked in the colonies of *C. herculeanus*. All foraging workers were marked in colonies of *F. exsectoides*. *F. fusca* had few foraging workers and the samples were obtained by removing all workers that emerged from the nest over a continuous period. The ants were marked on the dorsum of the thorax with a "Techpen." Unless otherwise stated, resampling was by counting all the ant in the forage area and not by removing a sample of a given size.

## OBSERVATIONS

The number of workers of *F. fusca* in the forage area was extremely low, varying from 0 to 13 at any given time. As only 30 of 3000 workers were marked the figures obtained were very variable and were not considered satisfactory for use in the Lincoln Index formula. Therefore, the totals of nine hourly readings were used and gave estimated populations of 193, 240, 95, 300 and 1080 on the five days following marking.

A spot check on the foraging population of this nest one month later gave 22 unmarked ants and none marked. A ten-minute count of all ants leaving the nest at this same time gave 71 unmarked and none marked.

The calculated and actual populations of three colonies involving *F. exsectoides* and *C. herculeanus* are shown in Table I. Table IIa shows the total number of marked and unmarked ants present in the foraging area during five days sampling of a colony of 2300 *C. herculeanus* in which 50 workers were marked. Table IIb shows the calculated populations based on the data presented in Table IIa.

TABLE I
Colony Size as Calculated from the Lincoln Index Compared to the Actual Size

| Species | No. of Ants Marked | Interval to Resampling | Sample | | Estimated Population | Actual Population |
|---|---|---|---|---|---|---|
| | | | Total No. of Ants | No. of Marked Ants | | |
| *Formica exsectoides* | 25 | 24 hrs. | 50 | 7 | 179 | 1200 |
| | | 5 days | 35 | 4 | 219 | 1200 |
| | | 6 | 35 | 7 | 125 | 1200 |
| *Formica exsectoides* | 15 | 6 days | 25 | 11 | 34 | 300 |
| *Camponotus herculeanus* | 40 | 20 hrs. | 76 | 28 | 109 | 3000 |
| | | 24 hrs. | 74 | 24 | 123 | 3000 |

Immediately after these samples on *C. herculeanus* were taken, the colony was transferred to another nest by dumping it into a new forage area, thus effecting a complete mixing of all workers. Two hours later 36 marked workers were among 259 that remained in the forage area. The population calculated from these figures was 371, which is within the range of calculated populations as shown in Table IIb.

## Discussion

Under these experimental conditions about 80 per cent of the ants in colonies of the three species studied do not forage; hence there is some division of labour among the workers. In some ants, particularly those with dimorphic worker castes, division of labour is well known. Extreme modification of the workers limits

TABLE IIa

NUMBER OF MARKED (M) AND UNMARKED (U) ANTS IN THE FORAGE AREA OF A COLONY OF CAMPONOTUS HERCULEANUS THAT CONTAINED 50 MARKED WORKERS

| Time | Days from Time of Marking | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| | M | U | M | U | M | U | M | U | M | U |
| 9 a.m. | 37 | 162 | 25 | 149 | 26 | 137 | 37 | 151 | 33 | 182 |
| 10 a.m. | 32 | 197 | 35 | 171 | 30 | 132 | 32 | 172 | 27 | 154 |
| 11 a.m. | 40 | 153 | 31 | 143 | 33 | 178 | 29 | 163 | 39 | 145 |
| 12 a.m. | 34 | 147 | 37 | 156 | 32 | 152 | 27 | 157 | 31 | 122 |
| 1 p.m. | 31 | 136 | 32 | 135 | 37 | 167 | 28 | 177 | 28 | 123 |
| 2 p.m. | 33 | 185 | 29 | 161 | 41 | 183 | 29 | 124 | 29 | 147 |
| 3 p.m. | 39 | 131 | 47 | 198 | 29 | 196 | 33 | 113 | 30 | 163 |
| 4 p.m. | 37 | 142 | 42 | 121 | 26 | 173 | 33 | 136 | 31 | 147 |
| 5 p.m. | 34 | 123 | 36 | 146 | no data | | 35 | 142 | 27 | 152 |

Average number of workers in forage area = 186.07 ± 3.42

TABLE IIb

POPULATIONS OF A COLONY OF 2300 CAMPONOTUS HERCULEANUS AS CALCULATED BY THE LINCOLN INDEX FROM THE DATA IN TABLE IIA

| Time | Days from Time of Marking | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| 9 a.m. | 269 | 348 | 313 | 254 | 326 |
| 10 a.m. | 358 | 294 | 270 | 319 | 335 |
| 11 a.m. | 241 | 281 | 320 | 331 | 236 |
| 12 a.m. | 266 | 261 | 288 | 341 | 247 |
| 1 p.m. | 269 | 261 | 276 | 366 | 270 |
| 2 p.m. | 330 | 328 | 273 | 264 | 303 |
| 3 p.m. | 218 | 261 | 388 | 221 | 322 |
| 4 p.m. | 242 | 194 | 383 | 256 | 287 |
| 5 p.m. | 231 | 253 | no data | 253 | 331 |

Average calculated population = 288.14 ± 6.94

them to one or few duties (Wilson, 1953). Division of labour is less clearly marked in species with a monomorphic worker caste. Chen (1937) showed that workers of *Camponotus* of different sizes tend to perform different duties but all were capable of performing the same task. Dobrzanska (1959) obtained similar information for the genus *Formica*. Physiological, rather than size, differences, largely determine the duties of the individual. The Lincoln Index is not a satisfactory means of estimating complete colony size where such physiological differences exist and promote a division of labour within a worker population.

In the individual experiments the number of *F. fusca* in each sample was very low, and thus no attempt was made to analyse the data statistically. The variation in estimated population could have been a reflection of natural variation in the behaviour of individuals. However, the infinite population, as would be calculated from the data one month later, probably resulted from a combination of the loss of marking compound and a change in behaviour of individuals. Some marked workers could still be found but all were in the cooler portions of the nest. (Marking trials with spiders have shown that ''Tech-pen'' ink will adhere for one year (A. L. Turnbull, personal communication) but its usefulness with these three species of ants was found to be limited to 10 days. The reciprocal cleaning activities of the workers resulted in complete removal of the ink in a period of 2 to 3 months.)

In *F. exsectoides* and *C. herculeanus* essentially the same groups of individuals were engaged in foraging for at least six days. In *C. herculeanus,* not only did the same group of individuals forage, but, under constant temperature and humidity, the number of foragers remained relatively constant. The small variation in these data (Table IIa) suggests that a correction factor might be applied to the samples to give a more accurate estimate of the population. However, a correction factor applied to the extremes in the data gives a 100 per cent difference (1552–3104) in estimated population. Hence, despite the accuracy of a number of samples, one sample would be unreliable. It would not be feasible to take samples every hour in the field as the ants returned from the first sample would not be completely redistributed in the population in time to take the second sample.

Samples from the field can be expected to be more variable than those obtained in the laboratory. Temperature, humidity, and other meteorological factors influence the number of ants foraging. Talbot (1943) showed that within certain temperature ranges the number of foraging workers of *Prenolepis imparis* Say may increase by six times with five degree change in temperature. Changes of similar magnitude were also shown for species of *Formica, Lasius,* and *Myrmica* with ten degrees change in temperature (Talbot, 1946). On the other hand Talbot's studies also showed that changes of 5 to 10 degrees within different temperature ranges had little effect on the number of ants foraging. There would be a different dilution of marked among unmarked workers if samples were taken at a different temperature than that at which the ants were marked.

Steyn (1954) showed that the effects of temperature and humidity caused a seasonal division of labour in colonies of *Anoplolesis custodiens* Smith and that at certain times one caste was excluded from foraging. During the winter only the smaller workers continued to forage; the larger became hibernating fat-repletes. This behaviour pattern would seriously affect the mix-

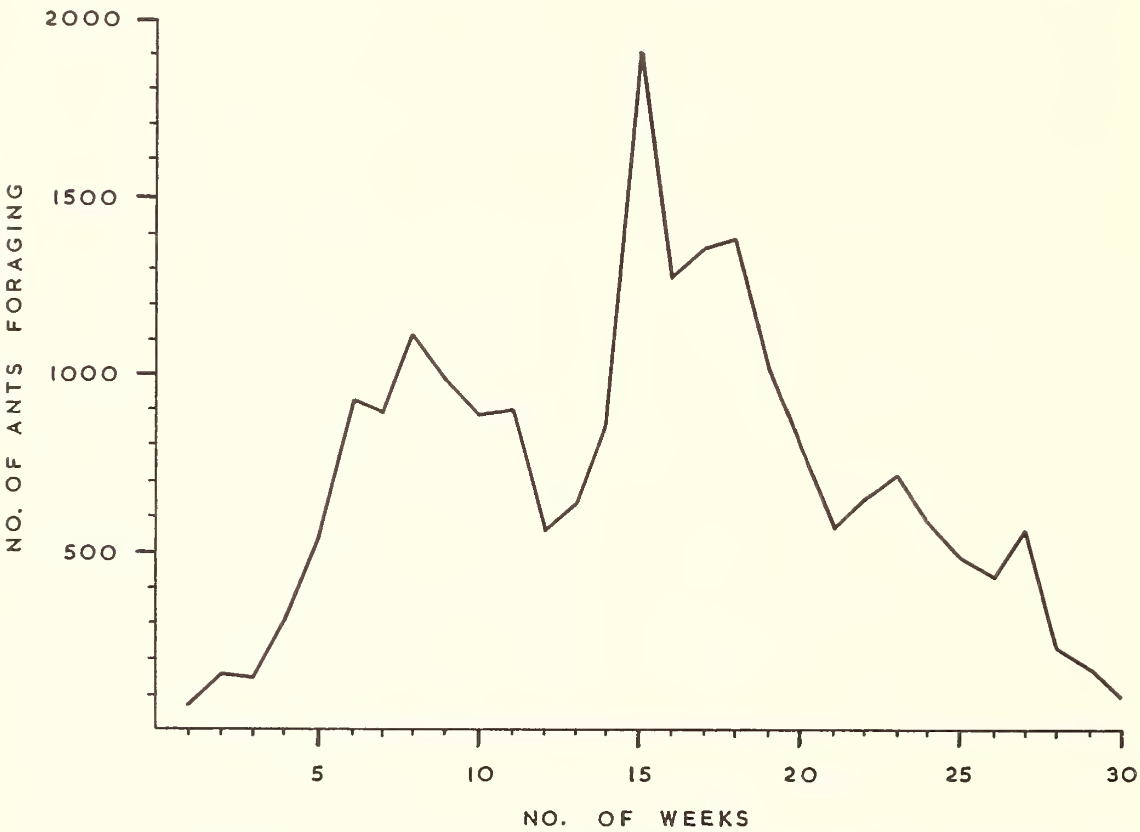


Fig. 1. Numbers of *Formica exsectoides* Forel foraging during a 30 week period.

ing of individuals in the colony and the percentage of the colony foraging would vary with the season.

The state of development of the brood affects the number of ants foraging and therefore the degree of mixing of marked and unmarked ants. The number of *F. exsectoides* leaving a rearing nest during a 10 minute period was recorded at 9 a.m., 1 p.m., and 5 p.m. each day from Monday through Friday for the entire foraging season. Temperature and humidity were constant throughout the entire period. The weekly totals of these data are shown in Figure I. The peak in activity that occurred eight weeks after establishing the colony represents the period of greatest food consumption by the larvae. The subsequent decline in activity occurred when the larvae pupated. The gradual increase beginning in the 12th week and the sudden increase in the 14th week correspond to the time of worker emergence. As the callow workers do not forage, the variation in the forage population to that time represents variation in the behaviour of individuals in the initial population. The presence of a brood stimulates not only the activity of individuals already foraging but also that total number of ants foraging (Vowles, 1953). This increase may be caused directly by stimuli from the brood or indirectly by stimuli from the more active workers (Chen, 1937).

The location where the foraging workers are sampled can affect calculations for total population. Samples taken at the nest opening or in the immediate vicinity of the nest would contain a high portion of workers that are engaged in constructing, cleaning, or repairing the nest. Samples taken in the general forage area of the nest would contain a high portion of ants that are engaged in foraging for insect food or in gathering honeydew. Dobrzanska (1958) showed that in certain species of *Formica* there is a partitioning of the forage area and that the workers may even confine their activities to single trails for limited periods. Dobrzanska, however, also showed that there is apparently no partitioning of the forage area in certain species of *Lasius, Tetramorium, Myrmica,* and *Leptothorax,* but she did not indicate if certain ants confine themselves to certain duties. These differences in foraging behaviour further point out the difficulties to be encountered when the Lincoln Index is used as a sampling technique for ants.

## Conclusion

Some of the problems involved in estimating the size of ant colonies are discussed. Unless one has a considerable knowledge of the foraging behaviour of the ant species concerned the index can give inaccurate or misleading results. However, the index may have an application to ants in comparative studies between colonies, of the same species, in showing variation in foraging activities of the one colony, and, as suggested by Chew, in showing colony growth. It must be kept in mind that data obtained in this manner is relative and does not necessarily indicate the actual numbers of ants in the colonies.

## ACKNOWLEDGMENTS

The author wishes to thank Miss M. Narusevicius for assistance in sampling the ant colonies used in these experiments.

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